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Responses of soil respiration to rainfall addition in a desert ecosystem: Linking physiological activities and rainfall pattern

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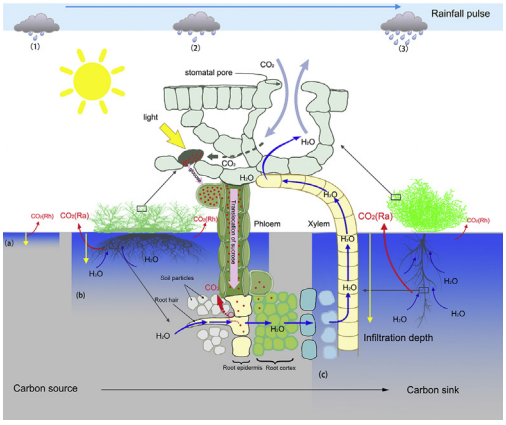
HIGHLIGHTS

- A rainfall simulation experiment was performed with two co-existing desert plants.
- Photosynthesis, soil respiration, predawn water potential, soil temperature and soil moisture were measured.
- We examine the effects of rainfall pattern on R_s and physiological responses of the two plants.
- Rainfall pattern–driven changes in R_s composition interact with physiological activity and abiotic factors.

GRAPHICAL ABSTRACT



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ABSTRACT

The tight linkage between photosynthesis (A_n) and soil respiration (R_s) has been verified in many terrestrial ecosystems. However, it remains unclear whether this linkage occurs in desert ecosystems, where water is considered an important trigger of carbon cycling. A field experiment was performed under seven simulated rainfall amounts (*0*, *3*, *5*, *10*, *15*, *25*, and *40* mm) with two co-existing desert plants (*Reaumuria soongorica* and *Nitraria sphaerocarpa*) in June (early growing season, *EGS*) and August (middle growing season, *MGS*) in 2016. A_n, R_s, predawn water potential (Ψ_{pd}), soil temperature (T_s) and soil moisture (S_{wc}) were measured for each treatment or control plot for 3 weeks. Our objective was to examine the effects of rainfall pattern on R_s and physiological responses of the two plants and the relationships between R_s and biotic and abiotic factors. No obvious variations in Ψ_{pd} or A_n were found under small rainfall events. However, when the rainfall amount exceeded *10* mm, both plants responded strongly, and the response patterns of R_s showed trends similar to those of A_n, which varied between species and seasons. Moreover, rain additions of *3–40* mm significantly increased R_s, and the relative changes in R_s (ΔR_s) of both species were much larger in the *EGS* than in the *MGS*. Importantly, abiotic factors may have controlled the variations in R_s under small rain events while A_n played a more important role in

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regulating the variations in R_s when the rainfall amount exceeded *10* mm for both species, suggest that the rainfall pattern–driven changes in R_s composition interact with physiological activity and abiotic factors to regulate the response of R_s to rainfall variability in desert ecosystems. Thus, climate change in the coming decades may lead to carbon sequestration by desert plants, which may cause desert ecosystems to act as carbon sinks.
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1. Introduction

Soil respiration (R_s) is the largest flux of CO_2 withdrawal from terrestrial ecosystems and thus will serve as a major determinant of ecosystem carbon balance under future climate change (Bond-Lamberty and Thomson, 2010; Davidson and Janssens, 2006; Rustad et al., 2000; Schlesinger and Andrews, 2000). Generally, R_s consists of autotrophic respiration by roots and heterotrophic respiration stemming from the decomposition of substrates by soil microorganisms (Kuzyakov, 2006), which, like all biochemical reactions, are highly temperature dependent (Raich and Potter, 1995). However, an increasing number of studies have illustrated that quantifying R_s based solely on environmental drivers such as soil temperature (T_s) makes predictive models of terrestrial carbon cycling inaccurate for the quantification of carbon fluxes (Erica et al., 2010; Vargas et al., 2011), since R_s is out of phase with T_s in most ecosystems, especially those with taller vegetation (Tang et al., 2005). Thus, the inconsistent relationships between R_s and abiotic factors indicate that other factors may play more important roles in controlling R_s, and such factors are likely determined by vegetation type-dependent plant physiological processes (Kuzyakov and Gavrichkova, 2010).

The tight linkage between photosynthesis (A_n) and respiration fluxes has been reported recently with the use of isotope tracing or eddy covariance methods in diverse ecosystems across multiple spatial and temporal scales (Bahn et al., 2009; Carbone and Trumbore, 2010; Högberg et al., 2001; Kayler et al., 2010; Kuzyakov and Gavrichkova, 2010). For example, Han et al. (2014) found that changes in R_s were strongly correlated with changes in ecosystem A_n between sunny days and adjacent cloudy days under the same T_s in a costal wetland. Stem girdling led to a 27% and 37% decrease in R_s compared with a corresponding control treatment in a boreal tree species (*Pinus sylvestris*) in early and late summer, respectively (Högberg et al., 2001). Additionally, this close link between A_n and R_s has been widely documented in steppes (Yan et al., 2011), crops (Moyano et al., 2007), and forests (Moyano et al., 2008; Tang et al., 2005). Theoretically, A_n influences the autotrophic component of R_s through the allocation of assimilates below ground and influences the heterotrophic component of R_s by transferring photoassimilated carbon via root exudation and associated mycorrhizal fungi (Kaiser et al., 2015). However, unlike in other ecosystems, it is still unclear whether this relationship occurs in arid ecosystems, where the activities of biota are dormant most of the time due to the harsh environment, water is considered one of the most critical factors controlling R_s (Huxman et al., 2004; Wu et al., 2016b). For example, Wang et al. (2013) reported that R_s was correlated positively with T_s and is regulated by the soil water content (S_{wc}) in a desert ecosystem. Another study showed that the vegetation may regulate the response of R_s to rain addition treatments (Song et al., 2012); however, whether the plant physiological activity influences R_s largely depends on the rainfall patterns since the plant physiological activities might not be triggered until threshold precipitation event. Thus, to reveal the relationship between A_n and R_s, it is prerequisite to determining the responses of plant physiological activities to rain events.

In the water-limited ecosystems, the biological activity is preliminarily driven by discrete precipitation pulses with different amounts of rainfall distributed across the growing season (Huxman et al., 2004). Specifically, small precipitation events may wet only the top few centimetres of arid soils and favored the microorganisms there, while precipitation from larger events could reach the root zone and stimulate plant physiological activities (Austin et al., 2004; Parton et al., 2012; Schwinning and Ehleringer, 2001; Wu et al., 2016a). However, the rainfall amounts needed to initiate the physiological activities vary among species and regions. For example, a previous study reported that graminoids respond more rapidly to rainfall events (as small as *5* mm) than woody plants (Thomey et al., 2015), while for desert regions, even *1* mm of rainfall can significantly increase sap flow in woody plants (Zhao and Liu, 2010). Moreover, according to the 'Buck model' developed by Knapp et al. (2008), larger precipitation events will extend the period without water limitation for ecosystems, which is associated with higher A_n and R_s, leading to a net C gain in water-limited systems. Furthermore, in addition to the size of the rainfall events, the seasonal variability in rainfall events may have the potential to modify the current states of plants and microbes, further influencing the carbon cycling in desert ecosystems (Huxman et al., 2004). However, most previous studies were mainly focused on the response of plant parts to rain pulses from either aboveground or belowground perspectives (Cheng et al., 2006; Ma et al., 2012; Song et al., 2012; Yang et al., 2014), while limited information is available on the link between the integrated plant system and rainfall pattern when considering the responses of R_s to rainfall addition, and whether an influential relationship occurs between aboveground and belowground based on field study, which constrains our understanding of the consequences of shifting precipitation regimes for the carbon balance in desert ecosystems, particularly under a more extreme climate (Al and Paasche, 2007).

To fill these knowledge gaps, we performed a series of rainfall simulation during the growing season in 2016 in a desert ecosystem co-dominated by *Reaumuria soongorica* and *Nitraria sphaerocarpa* to answer the following questions: 1) How do rainfall amount and seasonal variability affect R_s and plant physiological activities in two desert shrubs? 2) What are the relationships of R_s with A_n and environmental factors?

2. Materials and methods

2.1. Study site

The experiments were conducted in a desert ecosystem of the Heihe River Basin (HRB), Pingchan Town, Linze County, in the middle of The Hexi Corridor region of Gansu Province, at the southern edge of Badain Jaran Desert, northwestern China (39.4°N, 100.12°E) (Fig. 1). The local climate is a temperate continental desert climate with hot, dry summers and cold winters. The mean annual temperature ranges from 7.9 to 9.1 °C. The mean annual precipitation over 1961–2011 was 112 mm, approximately 80% of which occurred during May–September. Approximately 86% of the total number of rainfall events were precipitated <5 mm, and these small rainfall events accounted for ~42% of the total rainfall (Fig. S1). The soil texture is fine sand (according to the USDA), with a sand content of 90.5%, a silt content of 8.4% and a clay content of 1.1%. The soil organic matter within the top 1 m of soil is 42.8 g kg^{-1} on average, while the total nitrogen is 1.4 g kg^{-1} (Zhang et al., 2017). The dominant species are *Reaumuria soongorica* and *Nitraria sphaerocarpa* with vegetation covers of 2.6% and 5.4%, respectively. *R. soongorica* exhibits a sporadic distribution, while *N. sphaerocarpa* is interspersed on sand dunes. Both species are widely distributed from the middle to lower reaches of the HRB and exhibit characteristics typical of arid/semiarid region plants such as strong drought

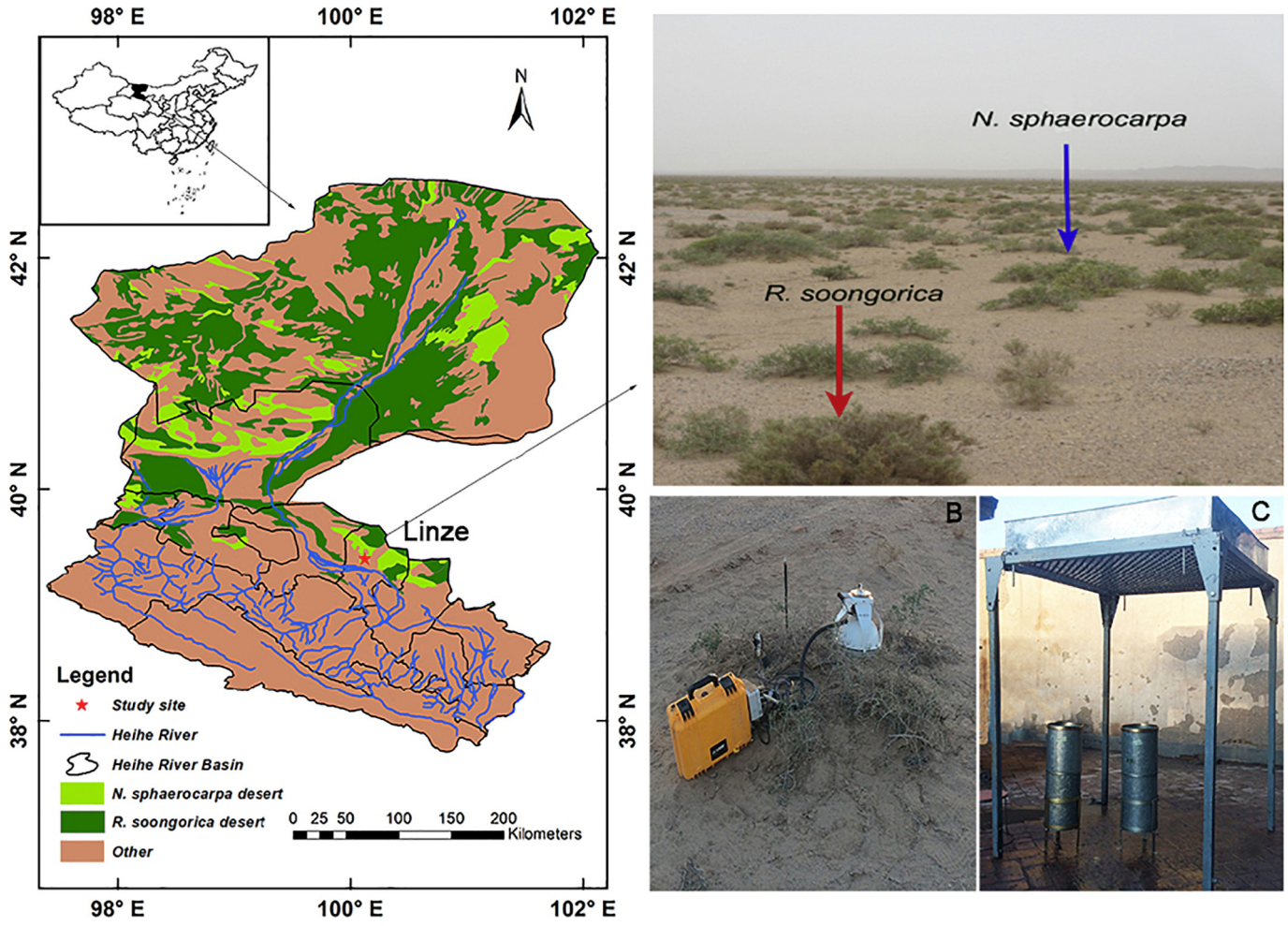

Fig. 1. The location of the study site in the Heihe River Basin. A: The landscape of the study site; B: A measurement conducted during the study period; C: The needle-type artificial rainfall simulator and rain gauge.

resistance, salt tolerance, heat resistance and sand stabilization (see Zhang et al. (2017) for more details on the two species).

2.2. Experimental design

Two large plots (50 × 50 m) containing both *N. sphaerocarpa* and *R. soongorica* were randomly selected at the study site. Within each large plot, 14 subplots (1 × 1 m) with canopy in similar size were selected and labelled for each species separately, giving a total of 28 1 m × 1 m subplots in each large plot, each of the subplots contained one individual of *N. sphaerocarpa* or *R. soongorica*. Seven levels of single rainfall events, namely, *0* mm (*CK*), *3* mm, *5* mm, *10* mm, *15* mm, *25* mm and *40* mm, were imposed randomly on the 14 labelled subplots for each species. Thus, there were two replications of a given rainfall event for each species in each large plot.

The manipulated rainfall events were determined according to the frequency of rainfall events determined from the climate data for 1961 to 2011 (Fig. S1). Given that phenological and rainfall pattern during the growing season, rain addition was applied separately in the early growing season (*EGS*, 26th of June) and middle growing season (*MGS*, 4th of August) in 2016 (Fig. S2). The distance between adjacent subplots was great enough to avoid the influence of different treatments. The water was pumped into a tank from a well near the study site only replenished by natural rain and then applied using a rainfall device to simulate rainfall (Fig. 1). The device was a needle-type artificial rainfall simulator with a 1 m × 1 m square gauge and a 1.5-m-high of iron rack. The bottom of the gauge consisted of 761 small rainfall systems (staggered arrays with 20 × 20 odd rows and 19 × 19 even rows); each of the rainfall systems was composed of a soft rubber stopper made of waterproof material and a medical injection needle and delivered water droplets uniformly over the treatment area. The time over which each rainfall amount was applied was determined by two standard rain gauges. The rainfall intensity was adjusted to be slow enough to prevent runoff. During the rainfall simulation, the device was wrapped with a transparent plastic cloth to avoid the influence of wind. To both minimize soil evaporation and allow full infiltration, the water treatments were carried out at night when the near-surface air was relatively cool and stable. Thus, the rain treatments implemented with the device simulated the future scenarios of increased rain events in this arid region.

2.3. Measurements of soil respiration and abiotic factors

Two PVC soil collars (7 cm high and 20 cm in diameter) were inserted under the canopy to a depth of 5 cm in each subplot one week before measurement to avoid the effect of soil disturbance on R_s and left in the same locations throughout the study. An Automated Soil CO_2 Flux System (LI-8100, LI-COR Inc., Lincoln, NE, USA) was used to manually measure R_s one day before the rain treatments and 1, 2, 3, 7, 11, 15 and 21 days after the rainfall addition. All the measurements were conducted between 9:00 am and 11:00 am local time. For each measurement, the chamber was placed firmly on each collar, and R_s was calculated automatically (linear or exponential regression) by increasing CO_2 concentration over 100 s after rejecting a "dead band" of the first 20 s and recorded by the software that accompanied the

instrument. For each PVC collar, the measurement was repeated twice before the next collar was measured.

T_s and S_{wc} were recorded in parallel during R_s measurements near each collar at 5 cm soil depth with a LI-COR thermocouple and moisture probe. Subsequently, we determined the soil moisture per unit volume of soil based on soil bulk density and S_{wc} using the oven-drying method. We employed the following equation to examine whether rain addition treatments significantly affected the response variable by comparing the response variable to that in the CK plot (Song et al., 2012):

$$\Delta X = \frac{1}{n}\sum_{i=1}^{n}\left((X_i - X_0)_{treat} - (X_i - X_0)_{ck}\right) \quad (1)$$

where X_i is the response variable such as soil respiration (R_s), photosynthetic rate (A_n) and predawn water potential (Ψ_{pd}) on the given day after rain addition and X_0 represents the response variable one day before rain addition; the subscripts "treat" and "ck" represent the water addition treatment plots and the control plots, respectively; and n is the number of measurements after rain addition treatment. A positive or negative ΔX means the response variable increased or decreased in the rain addition treatment when compared with the control plot, respectively.

2.4. Measurements of predawn water potential and photosynthesis

Ψ_{pd} was measured before sunrise (between 4:00 am and 6:00 am) using a pressure chamber (1515D Pressure Chamber Instrument, PMS Instrument Company, Albany, Oregon, USA). The measurements were taken immediately after the twigs were removed from the plants to minimize the effects of water loss on Ψ_{pd}. Terminal branches with leaves were used to determine the Ψ_{pd}. For each set of measurements, three or four branches, one from each plant of a similar canopy size, were taken for each species. The mean Ψ_{pd} is reported for treatment and reference plots.

A_n was measured using a portable photosynthesis system equipped with a red-blue light source (LI-6400, LI-COR) under natural field conditions. A_n measurements were recorded on three or four plants of each species using mature and healthy leaves and averaged to obtain the mean A_n. A_n was measured taken between 9:00 am and 11:00 am to allow the measurements to be compared with those of R_s. The target leaves of the two species were labelled with tags before the treatments and used repeatedly throughout the experiment. The photosynthetic photon flux density (PPFD) was set to 1500 μmol m^{-2} s^{-1}, and the relative humidity and carbon dioxide concentration in the chamber were controlled to be similar to the ambient values during the measurements.

2.5. Data analysis

One-way ANOVA was used to detect whether $\Delta\Psi_{pd}$, ΔA_n, ΔR_s (see Formula (1)) were significantly different among different rainfall treatments. Three-way ANOVAs were used to examine the effects of rain addition time, rainfall amounts and species on the five response variables (i.e., R_s, T_s, S_{wc}, A_n and Ψ_{pd}) after each rain addition treatment. Linear or polynomial regression analysis was used to evaluate the possible relationships between R_s and various factors. All statistical analyses were performed using SPSS 20.0 (SPSS for Windows, Version 20.0, Chicago, IL, USA). The results were presented and regression equations were determined using Sigma Plot version 11.0 (2008, Systat Software Inc., Chicago, IL, USA).

3. Results

3.1. Changes in soil water content and soil temperature

S_{wc} increased significantly for both species with increasing rainfall amounts and then decreased in both the *EGS* and the *MGS* (Fig. S3). The variation in the magnitude and duration of S_{wc} for the two species was contingent on the amount of rain added. There was no significant difference in the mean S_{wc} between the two species or the treatment times; only rain addition treatment had a significant positive effect on the S_{wc} of the two species ($P < 0.001$, Table 1).

As the amount of added rain increased, T_s decreased more and the treatment-induced lower T_s persisted for longer (Fig. S4). All rain addition treatments significantly decreased T_s ($P < 0.001$, Table 1), which consequently influenced seasonal variation in T_s ($P < 0.05$, Table 1). However, there were no significant differences in T_s between the two species following the rain addition treatments ($P = 0.34$, Table 1).

3.2. Changes in predawn water potential and photosynthesis

Ψ_{pd} did not increase significantly in either of the species when the rainfall was *<10* mm (Fig. 2 and Table S1). Additionally, the relative change in Ψ_{pd} ($\Delta\Psi_{pd}$) showed no obvious difference between the rainfall addition treatment and the *CK* under small rainfall events (Fig. 3A for *N. sphaerocarpa*, Fig. 3B for *R. soongorica*), but as the amount of rainfall increased, the Ψ_{pd} of each species increased significantly, although the magnitude of the increase varied between species and the seasons (Fig. 2). Specifically, in the *EGS*, the peak of Ψ_{pd} occurred on the second day for *N. sphaerocarpa* when the rainfall amount was *≥10* mm, while the peak occurred on the third day for *R. soongorica* (Fig. 2A and C). However, the peak of Ψ_{pd} for the rainfall events with an amount *≥10* mm occurred 1 day earlier in the *MGS* than in the *EGS* for both species (Fig. 2B and D). Correspondingly, the response of A_n following the rain addition treatments showed patterns similar to those of Ψ_{pd} for both species because A_n and Ψ_{pd} were highly correlated ($R^2 = 0.80$ in *EGS* and 0.89 in *MGS* for *R. soongorica*, $P < 0.001$, Fig. S5A; $R^2 = 0.88$ in *EGS* and 0.89 in *MGS* for *N. sphaerocarpa*, $P < 0.001$, Fig. S5B). Specifically, there was no obvious increase in A_n ($P > 0.05$, Fig. 3A and B, Table S1) in either of the species when the rainfall was *<10* mm, but when the rainfall was *≥10* mm, the peak of A_n appeared in the same manner as that of Ψ_{pd} for both species (Fig. 4). In addition, the significant increase in the relative change in A_n (ΔA_n) corresponded to a significant increase in $\Delta\Psi_{pd}$ with increasing rainfall amounts (Fig. 3C for *N. sphaerocarpa*, Fig. 3D for *R. soongorica*). Overall, the species, rain addition time, and rain amount all had significant effects on Ψ_{pd} and A_n ($P < 0.001$ for both A_n and Ψ_{pd}, Table 1).

3.3. Responses of soil respiration to rain additions

R_s increased rapidly after each rain addition treatment and then weakened gradually until the next rainfall events occurred in all treatment plots (Fig. 5). When the rainfall was *≤10* mm, the peak of R_s always occurred on the first day after rain addition. However, when the rainfall was *>10* mm, the R_s peak did not exhibit a consistent pattern; instead, the pattern was contingent on the species and seasons. Interestingly, the peak of R_s occurred on the same day as that for A_n under a given rainfall treatment (Fig. 5A and B for *N. sphaerocarpa*, Fig. 5C and D for *R. soongorica*). During the growing season in 2016, the rain addition

Table 1
Results of three-way ANOVA of the effects of species (S), rain addition time (T), rain addition treatment (R) and their interaction on soil respiration (R_s), soil temperature (T_s), soil water content (S_{wc}), photosynthesis (A_n) and plant water potential (Ψ_{pd}) after rain addition treatments.

	df	R_s	T_s	S_{wc}	A_n	ψ_{pd}
		P	P	P	P	P
Species (S)	1	0.012	0.341	0.320	0.000	0.000
Time (T)	1	0.134	0.030	0.264	0.000	0.000
Treatments (R)	6	0.000	0.001	0.000	0.000	0.000
S * T	1	0.842	0.226	0.616	0.046	0.595
S * R	6	0.965	1.000	0.998	0.194	0.992
T * R	6	0.880	0.992	0.889	0.998	0.940
S * T * R	6	0.993	0.999	1.000	0.848	0.895

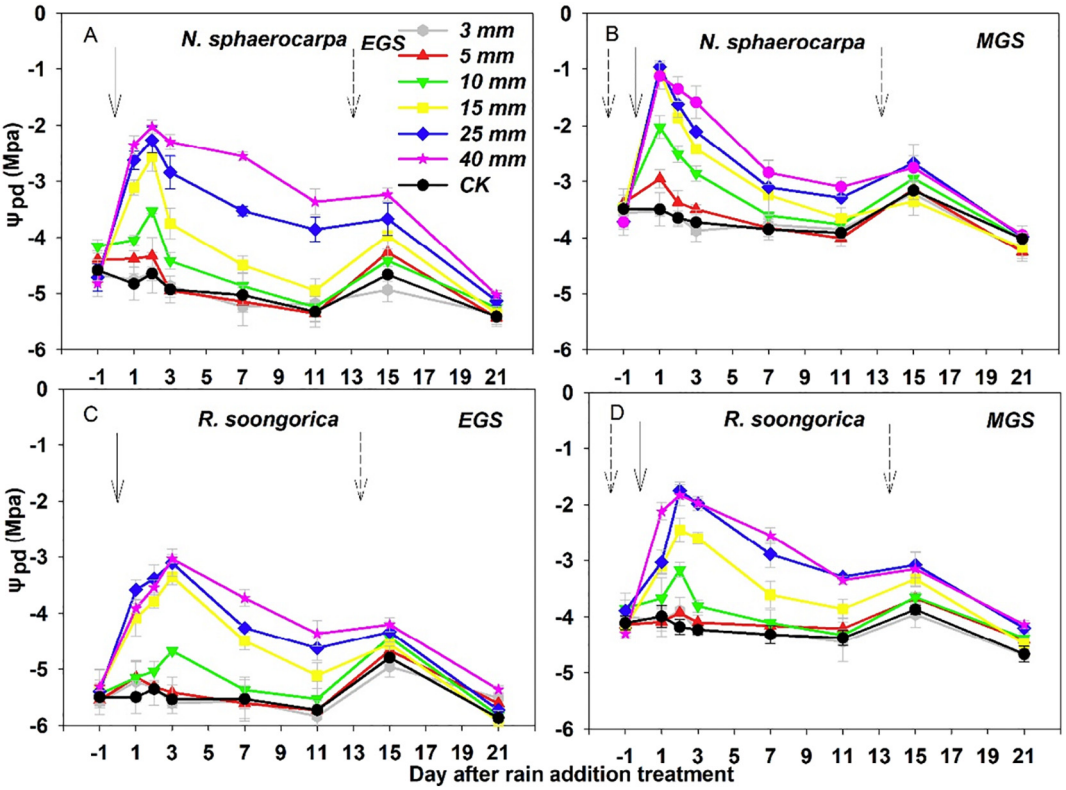

Fig. 2. Changes in plant water potential (Ψ_{pd}) following different rain addition treatments in the early growing season (*EGS*) and the middle growing season (*MGS*) for two desert species. Dotted arrows represent natural precipitation events, and solid arrows represent rain addition treatments. Error bars indicate ± 1 standard deviation.

significantly increased the relative change in R_s (ΔR_s) for both species (Fig. 3E and F).

3.4. Relationships between soil respiration, photosynthesis and abiotic factors

R_s increased with increasing A_n for both species, and exponential functions fit the relationships between R_s and A_n well (for *N. sphaerocarpa*, $R^2 = 0.70–0.82$, $P < 0.001$, Fig. S6A; for *R. soongorica*, $R^2 = 0.62–0.76$, $P < 0.001$, Fig. S6B). Similarly, a significant linear relationship was found between the ΔR_s and the ΔA_n for each species during the growing season (for *N. sphaerocarpa*, $R^2 = 0.65–0.68$, $P < 0.001$, Fig. 6A; for *R. soongorica*, $R^2 = 0.57–0.66$, $P < 0.001$, Fig. 6B); additionally, the ΔR_s showed greater sensitivity to ΔA_n in the *EGS* than in the *MGS* in both species, especially *R. soongorica*. The R_s increased significantly with increasing S_{wc} and then gradually became insensitive to S_{wc} in both species, especially in the *EGS*; further, polynomial functions fit the relationships between R_s and S_{wc} well in both the *EGS* and the *MGS* ($R^2 = 0.54–0.88$, $P < 0.001$, Fig. S6C and D). Exponential functions fit the relationship between T_s and R_s well ($R^2 = 0.35–0.69$, $P < 0.001$, Fig. S6E and F).

4. Discussion

4.1. Response of physiological activity to rain addition treatments

In this desert ecosystem, no obvious changes in Ψ_{pd} or A_n were found following small rainfall events (3 mm or 5 mm) during the *EGS* or the *MGS* (Figs. 2 and 4). This result was consistent with the previous finding that plants have no obvious physiological response to rainfall until a larger pulse or a series of small pulses occurs, especially deep-rooted woody shrubs in water-limited regions (Huxman et al., 2004; Reynolds et al., 2004). Indeed, 3 mm or 5 mm of rain in our study site wet only the top few centimetres of soil (infiltration depths <*10* cm, unpublished data) and that moisture was quickly lost due to high evaporation; thus, small rainfall amounts hardly changed the S_{wc} conditions surrounding the plant rhizosphere (the total roots, especially fine roots, of the two species are usually distributed below *10* cm, Fig. S7), which limits the ability of plants to take up rainwater before it evaporates (Flanagan et al., 2010). However, as the rainfall amount increased to ≥*10* mm, a so-called 'biologically important' event (Ogle and Reynolds, 2004a), both the species responded significantly, and the response patterns varied between species and seasons (Figs. 2 and 4). Specifically, we found that *N. sphaerocarpa* responded faster than *R. soongorica*, while *R. soongorica* had a longer duration of physiological activity in both the *EGS* and the *MGS* than *N. sphaerocarpa*. This difference was probably caused by the different distributions of root systems between the two species (Huxman et al., 2004). Shallow-rooted plants rely more on the dynamics of S_{wc} near the surface and have short periods of rapid physiological response, whereas deep-rooted plants respond slowly but with longer physiological activity due to their ability to access deep water reserves (Ogle and Reynolds, 2004a; Schwinning et al., 2002). For *N. sphaerocarpa* in our study site, the bulk of the root mass was distributed in the upper *80* cm both vertically and horizontally, while the root systems of *R. soongorica* generally penetrated much deeper (Fig. S7). This difference may partly explain why *N. sphaerocarpa* responded faster than *R. soongorica*, which was also found by Zhang et al. (2017) in the same region. In addition, we found that the delayed response of physiological activity of both species to rainfall addition was more intense but shorter in the *MGS* than in the *EGS*. This difference may be caused by the relatively wetter soil conditions in the *MGS* than in the *EGS* before rain addition (Fig. S3) because the level of pre-existing moisture may diminish or amplify the effect of an individual rainfall pulse on plant response, according to previous research (Ogle and Reynolds, 2004b). In addition, the close correlations among Ψ_{pd}, g_s, T_r, and A_n (Fig. S5) suggest that the plant physiological activities were strongly coupled in the desert ecosystems once physiological activity was triggered.

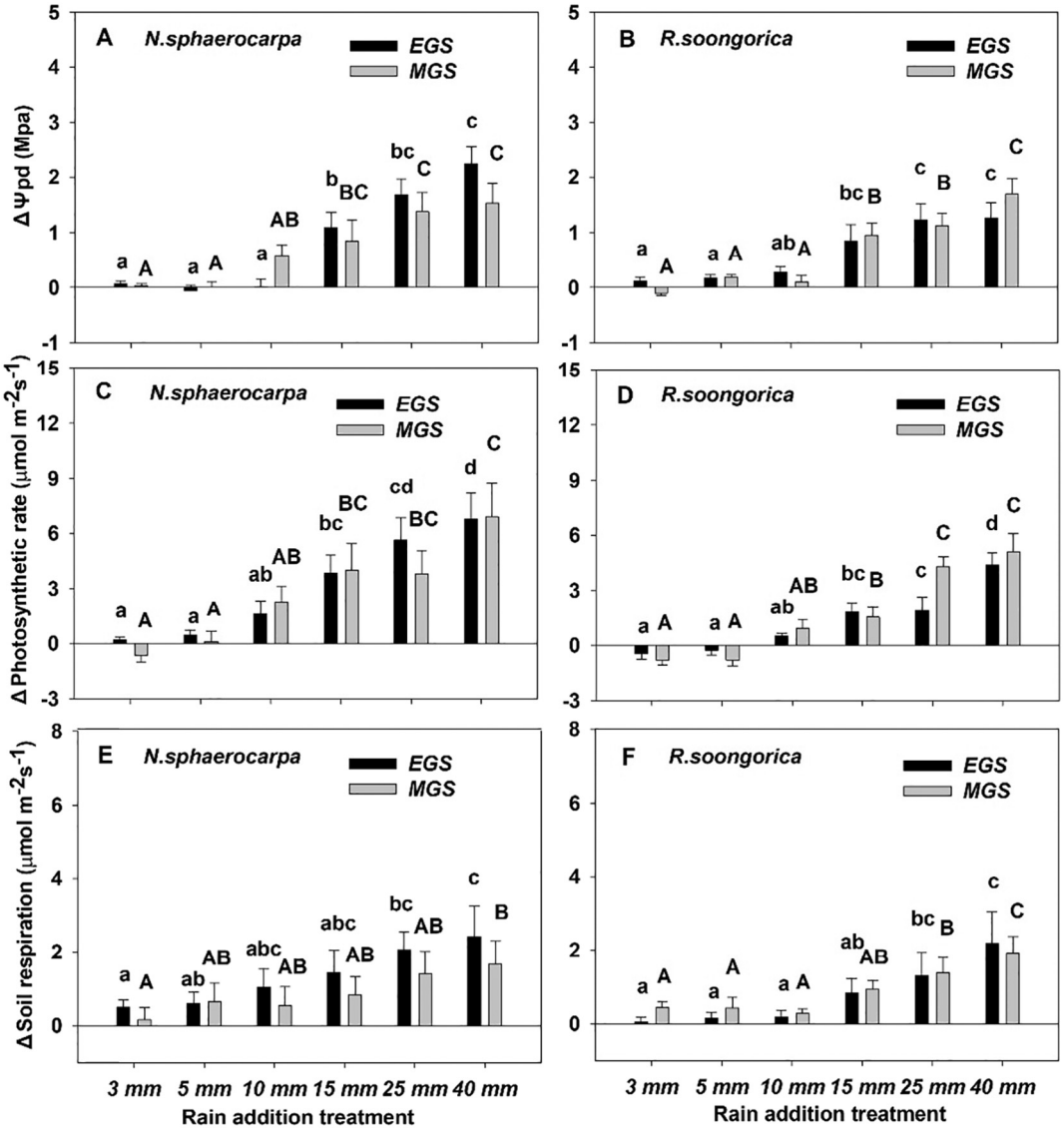

Fig. 3. The relative changes in soil respiration (R_s), photosynthetic rate (A_n) and predawn water potential (Ψ_{pd}) (see Formula (1) for the detailed calculation procedures) after rain addition treatments compared with the control plot (CK) for *N. sphaerocarpa* and *R. soongorica* in the early growing season (*EGS*) and the middle growing season (*MGS*). Data are the mean ± 1 SE (n = 6); different letters denote significant differences between rain addition treatments (uppercase for the *MGS*, lowercase for the *EGS*, one-way ANOVA, $P < 0.05$).

4.2. Response of soil respiration to rain addition

We found that rain additions of *3–40* mm all significantly increased R_s by approximately 1.58–9.08-fold times in the *EGS* and 0.12–2.01-fold times in the *MGS* for *N. sphaerocarpa* and by approximately 0.14–6.91-fold in the *EGS* and 0.23–3.03-fold in the *MGS* for *R. soongorica* relative to the *CK*. The importance of soil water availability for the carbon balance in desert ecosystems was already verified in previous studies (Cable et al., 2008; Chen et al., 2009; Huxman et al., 2004; Ma et al., 2012; Song et al., 2015; Sponseller, 2007; Unger et al., 2010). However, our study further showed that the response patterns of R_s were different depending on the rainfall amount (Fig. 5). Specifically, when the rainfall amount *≤10* mm, unlike Ψ_{pd} or A_n, R_s exhibited strong pulses followed by a subsequent peak, but the rate of R_s rapidly decreased to the pre-rainfall level until the next rainfall event. Previous studies reported this phenomenon, which was attributed to the physical displacement of CO_2-rich soil air and the quick response of microbial activity after the topsoil was rewetted (Austin et al., 2004; Huxman et al., 2004). However, we found that both the magnitude and duration of R_s were different when the rainfall amount was *>10* mm. More importantly, the pattern of R_s was similar to that of A_n (Fig. 4). The highly synchronous trends of A_n and R_s under rainfall events *>10* mm illustrated that A_n had a powerful effect on R_s when plant physiological activities were triggered. Additionally, we found that the ΔR_s of both species was much larger in the *EGS* than that in the *MGS*, which is similar to the findings of previous studies in desert ecosystems (Song et al., 2012) and other ecosystems (Inglima et al., 2009; Sponseller, 2007; Unger et al., 2010; Yan et al., 2010). These studies revealed that the rapid wetting of extremely dry soil could cause large amounts of CO_2 from soil due to enhanced microbial activity (Austin et al., 2004), while the drying-rewetting cycle could reduce the labile substrate, which may weaken the effect of rewetting on the heterotrophic components of R_s (Borken and Matzner, 2010; Cable et al., 2008). Our study showed that more natural rainfall events and a relatively higher S_{wc} occurred in the *MGS* than in the *EGS* (Fig. S3) before the rain addition treatments, which may partly explain the smaller increase in R_s in the *MGS* due to reduced soil nutrients caused by high microbial activity. In addition, ΔR_s was more sensitive to ΔA_n in the *EGS* than in the *MGS*, especially for *R. soongorica*, which illustrated that different belowground responses to photosynthetic substrate supply may also influence the R_s at seasonal timescales.

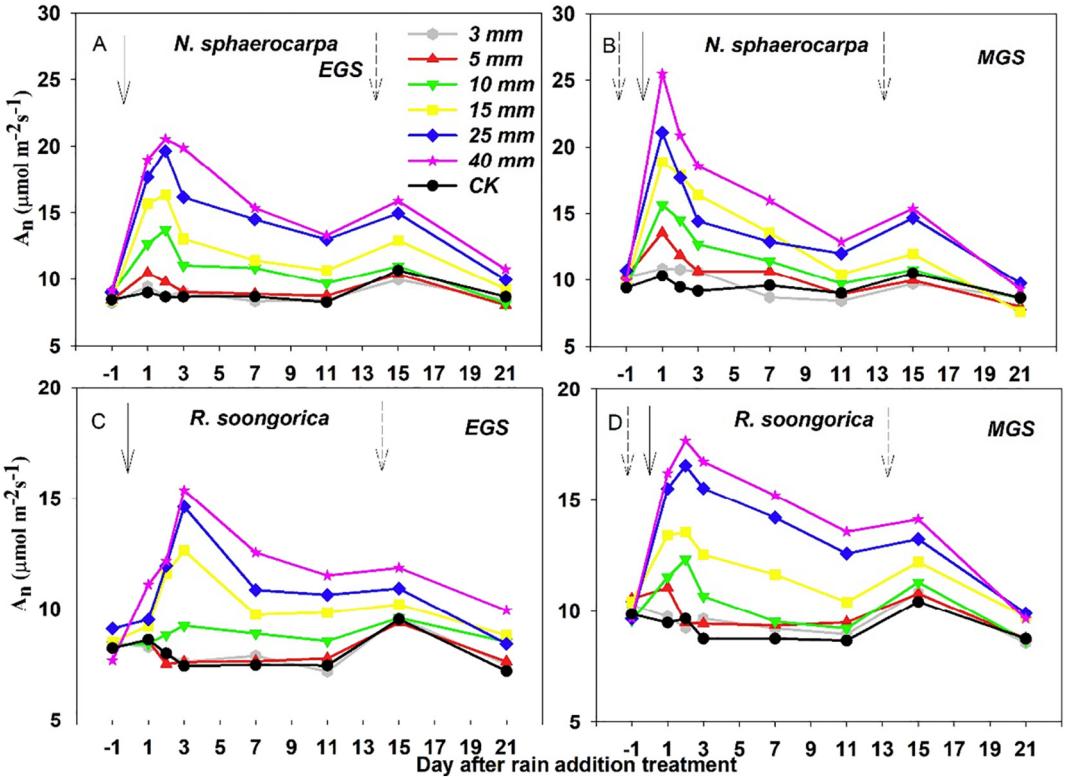

Fig. 4. Changes in photosynthesis (A_n) following different rain addition treatments in the early growing season (*EGS*) and the middle growing season (*MGS*) for two desert species. Error bars were removed to improve clarity. Dotted arrows represent natural precipitation events, and solid arrows represent rain addition treatments.

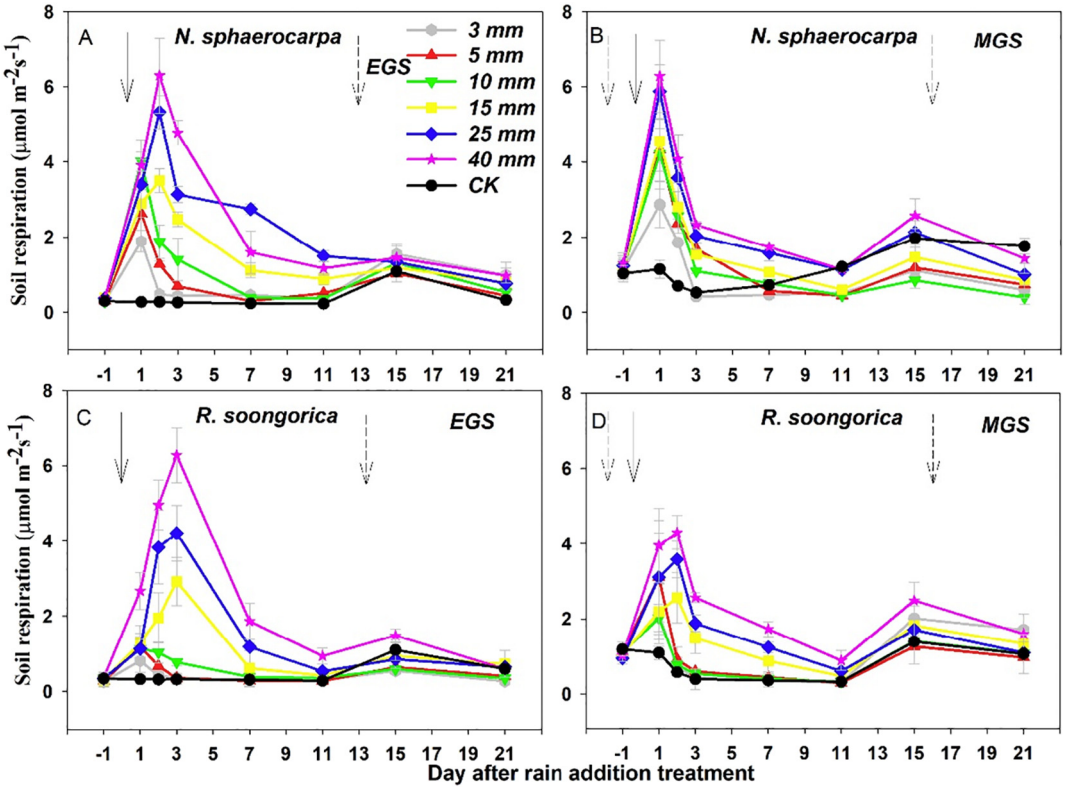

Fig. 5. Changes in soil respiration (R_s) following different rain addition treatments in the early growing season (*EGS*) and the middle growing season (*MGS*) for two desert species. Dotted arrows represent natural precipitation events, and solid arrows represent rain addition treatments. Error bars indicate ± 1 standard deviation.

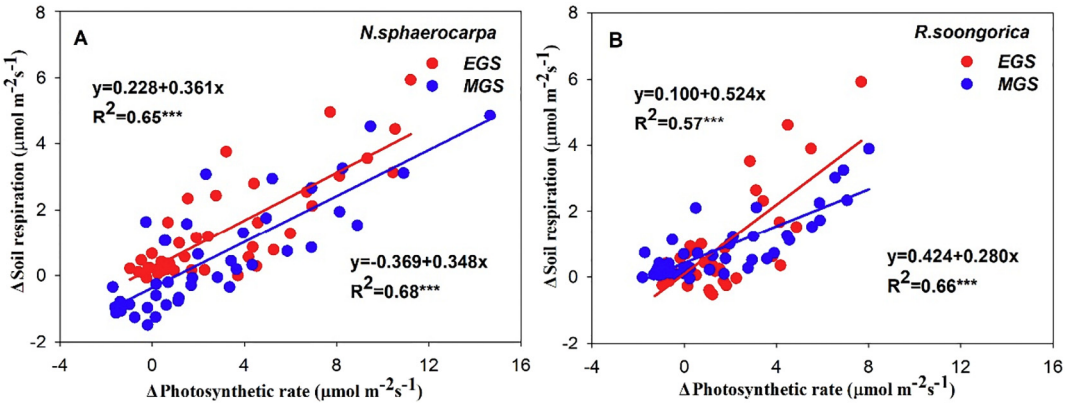

Fig. 6. The relative changes in soil respiration (R_s) versus photosynthetic rates (A_n) of two desert shrubs in the early growing season (*EGS*) and the middle growing season (*MGS*) following different simulated rainfall events (in mm). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

4.3. Relationships between soil respiration, photosynthesis and abiotic factors

Our study showed that the R_s of two species was positively correlated with A_n and S_{wc} and negatively correlated with T_s, indicating that abiotic and biotic factors co-regulate the response of R_s to rain addition (Fig. S6). Rain addition is known to mitigate drought stress in water-limited ecosystems by providing a favourable environment and more available resources for microbes and plants (Huxman et al., 2004). Additionally, S_{wc} could modify the temperature sensitivity of R_s and its components and synergistically affect the variations in R_s, results that have been reported in other arid and semiarid ecosystems (Liu et al., 2017; Song et al., 2015). However, the increased S_{wc} could also reduce R_s by restricting the diffusion of CO_2 out of soil and oxygen in to the soil (Sponseller, 2007). In addition, we found that both the magnitude and duration of R_s were regulated by the A_n, particularly under larger rainfall events (Fig. 5), suggesting that increased carbon assimilation is a critical driver of R_s; this effect was also verified by the significant linear relationships between ΔR_s and ΔA_n (Fig. 6). Aboveground A_n may influence respiration processes belowground in several ways. First, root respiration depends on the allocation of carbon assimilates to roots, which may be tightly linked with the A_n of the canopy (Yan et al., 2011). Second, the respiration of mycorrhizal fungi attached to roots has been found to be highly correlated with newly produced photosynthates (Heinemeyer et al., 2006). Third, root exudation of labile C could amplify the respiration of rhizosphere microorganisms by accelerating the decomposition of soil organic matter, which is also affected by the allocation of assimilates to roots (Kuzyakov and Domanski, 2015; Kuzyakov et al., 2000). However, the different responses of R_s, which were dependent on rainfall amount in our study, suggest that the influencing factors vary with rainfall amount: similar patterns were found variation for S_{wc} and R_s, while no obvious physiological activity response was detected under small rain events (*3* mm or *5* mm), implying that A_n will not influence R_s significantly and abiotic factors may have controlled the variations in R_s, mainly composed by heterotrophic respiration, under the small rainfall events. However, when physiological activity was triggered (*>10* mm in this study), A_n played a more important role in regulating the variations in R_s, mainly composed by autotrophic and heterotrophic respiration, until the combination of an extremely low S_{wc} and a high T_s limited the physiological activities of plants. Furthermore, as previously suggested, the level of pre-existing moisture which was highly dependent on the seasonal variability in rainfall events, may also diminish or amplify the effect of an individual rainfall pulse on R_s. Therefore, this study revealed the novel finding that rainfall pattern-driven changes in R_s composition interact with physiological activity and abiotic factors to regulate the response of R_s to rainfall variability in a desert ecosystem.

4.4. Impacts of changes in precipitation patterns on ecosystem C fluxes in a desert ecosystem

Precipitation patterns are expected to shift to more intense rainfall regimes (through extreme individual precipitation events) with longer intervening dry periods in the coming decades (Al and Paasche, 2007). Such a shift would reinforce or weaken the activity of different components of biota, further influencing community composition or even the structure and function of desert ecosystems. Based on the findings of this study, we introduce a conceptual framework linking rainfall pattern, the differential response of R_s components, and plant physiological activity to better understand the response of biota to precipitation regime change, which may enhance our ability to predict the changes in carbon fluxes of desert ecosystems (Fig. 7). Based on the long-term precipitation records of this region, approximately 42% of the total rainfall amount precipitated in amounts *<5* mm, and 86% of the total number of rainfall events fell into this category (Fig. S1). Our results showed that *3* mm or *5* mm of rain in our study site could trigger only soil heterotrophic respiration, illustrating that our study site may serve as a carbon source as reported by Sponseller (2007) for the Sonoran Desert, where the precipitation regime is also dominated by light rain events. However, except in one case: biological soil crusts (BSCs) on the topsoil, and autotrophic bacteria such as cyanobacteria will respire autotrophically which may reduce R_s, whereas there were no obvious BSCs in our study site. Altered precipitation regimes characterized by more extreme precipitation events with longer intervening dry periods would have more opportunities to trigger the physiological activities and carbon assimilation of plants. In addition, our study revealed more intense plant physiological activity but lower R_s in the *MGS* than in the *EGS* for both species, indicating that more carbon sequestration occurs in the *MGS* in the desert ecosystem. However, longer intervening dry periods will have critical consequences for soil water dynamics at both deep and shallow soil depths, and such alterations would favour the growth of plants with more deeply distributed roots (probably *R. soongorica*) and lead to longer physiological activity following a heavy rainfall event to gain net C due to the longer amount of time that water remains biologically available (Huxman et al., 2004). Hence, we speculate that climate change in the coming decades may facilitate carbon sequestration by desert plants, especially in the *MGS* and for plants with more deeply distributed roots such as *R. soongorica* in our study site, and will tend to cause desert ecosystems to serve as carbon sinks.

Our results have important implications for establishing mechanistic process models of R_s in desert ecosystems under future climate change. Given that the timing and magnitude of rainfall pulses may differentially affect the responses of R_s components, combining to influence the C balance of desert ecosystems, we emphasize the association of the effects of physiological activity with rainfall pattern when

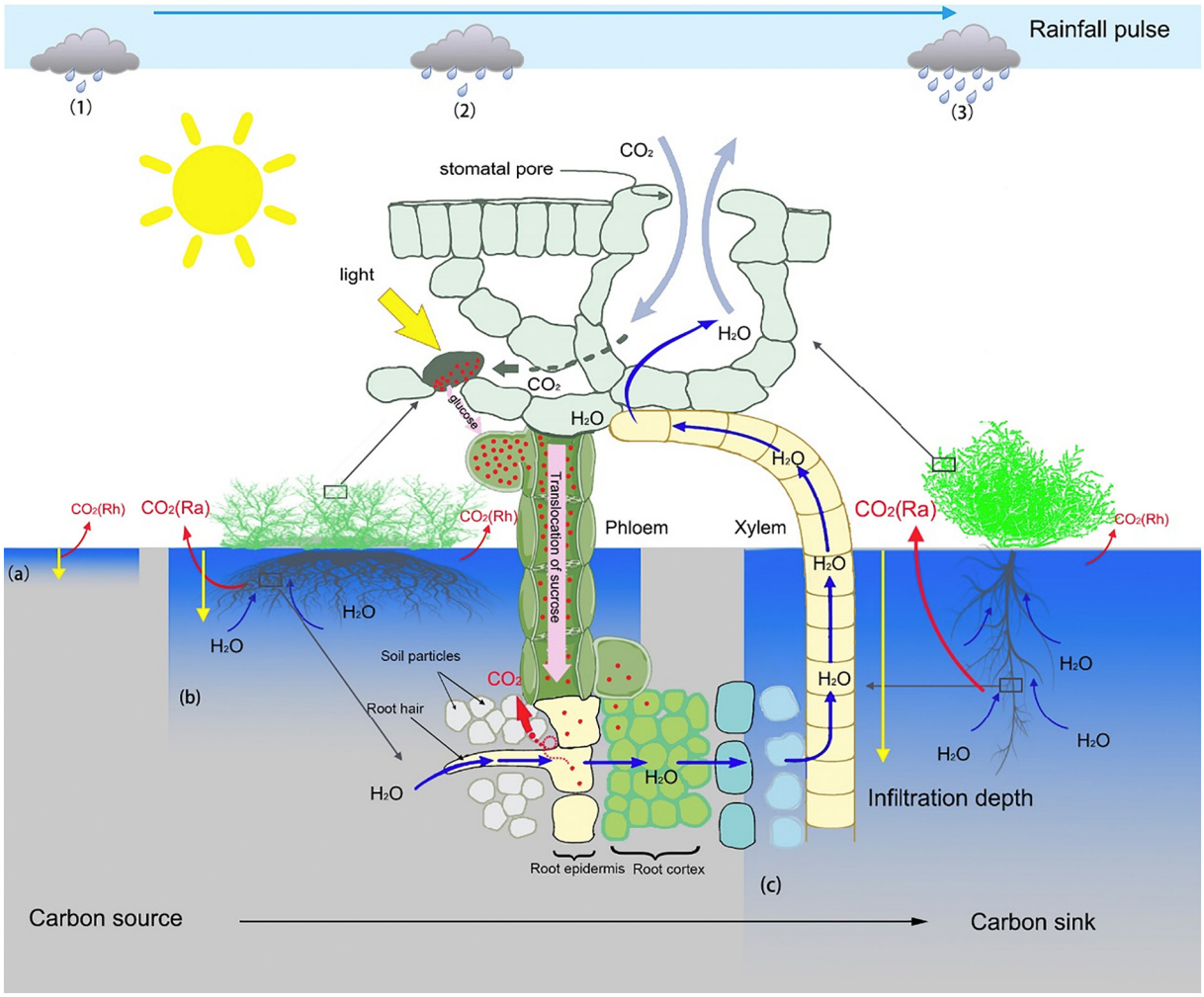

Fig. 7. C fluxes (red lines) in bare soil and sub-canopy areas and the possible changes in carbon stocks of desert ecosystems in the context of global climate change. The vertical yellow lines represent infiltration depths following different amounts of rainfall, and the lengths of red lines represent the duration of C fluxes. Three activity states are presented: (a) small rainfall events trigger heterotrophic respiration under bare soil and sub-canopy areas, (b) moderate rainfall events trigger microbial respiration and plant physiological activity of both shallow- and deep-rooted plants, and (c) larger rainfall events favour deep-rooted plants with longer physiological activity due to their ability to access deep water reserves; these activity states correspond to the three rainfall size classes represented by (1), (2), and (3). The phloem, used for water transport, and the xylem, used for product transport, are tightly coupled at the stomatal pore. R_h: heterotrophic respiration; R_a: autotrophic respiration.

considering the response of R_s to rain pulses both at local or large temporal and spatial scales, which could precisely predict the future roles of desert ecosystems in terrestrial C balance.

5. Conclusion

In this study, no obvious changes in Ψ_{pd} or A_n were found following light rainfall events (*3* mm or *5* mm) during the *EGS* or the *MGS*. However, when the rainfall amount exceeded *10* mm, both species responded significantly, and the response pattern varied between the species and seasons. In addition, we observed dramatic responses of R_s to rain addition in all treatment plots in both the *EGS* and the *MGS*. Importantly, the pattern of variation in R_s was similar to that in A_n when the rainfall amount exceeded *10* mm. Moreover, a significant linear relationship was found between ΔR_s and ΔA_n for each species during the growing season. Additionally, we found that the ΔR_s of each species was much larger in the *EGS* than in the *MGS*. The influencing factors of and variations in R_s following rain addition treatments depended on the rainfall pattern. Specifically, when the rainfall amount was below *10* mm, no obvious changes in Ψ_{pd} were found, and R_s was mainly affected by abiotic factor (T_s and S_{wc}). However, when the rainfall amount exceeded *10* mm, the magnitude and duration of R_s were regulated by both biotic (A_n) and abiotic factors. In conclusion, the rainfall pattern-driven changes in R_s composition interacted with physiological activity and abiotic factors to regulate the response of R_s to rainfall variability in a desert ecosystem.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.10.057.

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